THE LIFE EXPECTANCY OF THE WILD PIG *SUS SCROFA* L. IN RUHUNA NATIONAL PARK, SRI LANKA[1]

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(*With five text-figures and one plate*)

Key words: Age determination, cementum, life expectancy, mortality, life table, *Sus scrofa*, herbivores

A pick-up collection of skulls in Ruhuna National Park, made to determine age at death of ruminant herbivores through study of layering in the cementum of their molar teeth, also contained skulls with teeth of 29 adult wild pig (*Sus scrofa*). Layering present in the dentine of the tusks cannot be used to determine age. But layering in the cementum of the molars, although generally less clearly marked than in water buffalo (*Bubalus bubalis*), has permitted the determination of age at death in 23 specimens. The pattern of dark layers resembles that in *Bubalus*, with strongly and weakly marked lines alternating, corresponding with the major and minor dry seasons. It differs from that in sambar (*Cervus unicolor*) and chital (*Axis axis*) where a dark layer forms only in the main dry season each year. The mean life expectancy of young adults is 6.0 years and the maximum 12 years, with no evidence of distinction between the sexes, a situation very similar to that in the water buffalo. But juvenile mortality due to predation is dramatically greater in wild pig, compensated for by a correspondingly higher fecundity than in water buffalo. Sambar and chital both have longer life expectancies as adults than water buffalo or wild pig.

INTRODUCTION

The wild pig *Sus scrofa* L. is an adaptable omnivore distributed generally in the broad-leaved forest and steppe regions of the Palaearctic, extending through southern and southeast Asia to Java, Bali, Flores and the Solomon Islands (Honacki, Kinman and Koeppl 1982), and introduced as domestic or feral stock widely elsewhere. In Sri Lanka, as the sub-species *Sus scrofa cristatus,* it is a prominent mammalian component of the ecosystem, particularly in the dry zone of the country (Santiapillai and Chambers 1980, de Silva *et al.* 1995). This habitat is seen in a pristine form in Wilpattu and Ruhuna (Yala) National Parks (for location see Fig. 1). It is very active as an opportunistic feeder on the more succulent elements in the vegetation, particularly underground storage organs, and on carrion. Corpses are dismembered within a few hours of death.

Inspite of the richness of its fauna of mammals, as of other land vertebrates, there has been little study of the ecology of the mammals in southern and southeastern Asia. Schaller (1967) undertook a pioneering study of the ecological relations of the large herbivores and predators in Kanha National Park, Madhya Pradesh, as representative of the drier forests of peninsular India, including an outline analysis of the age structure of the large herbivores, but it could only concern indices of age as his estimates were based on tooth-wear alone. Eisenberg and Lockhart (1972) conducted an outline survey of the ecology of large mammals in Wilpattu National Park in Sri Lanka. This has been followed by more specific studies on the

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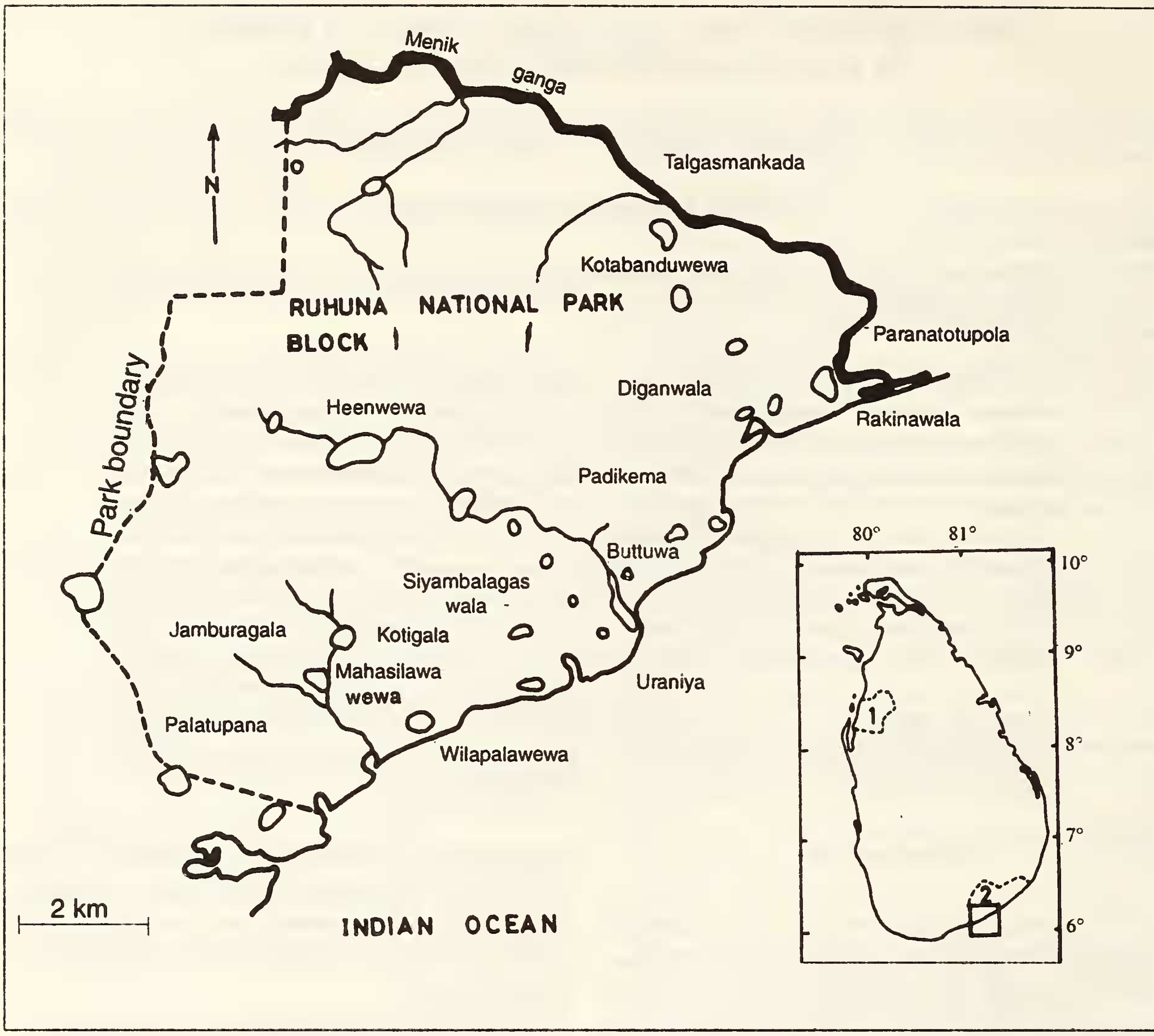

Fig. 1. The study area in Ruhuna National Park (Block I, the southwestern section), and the position of Wilpattu (#1) and Ruhuna (#2) National Parks in Sri Lanka.

population densities and annual breeding cycles of the large herbivores, and of the leopard *Panthera pardus* as the main large predator, in Block I, the southwestern part of the coastal section of Ruhuna National Park (Santiapillai *et al.* 1981, Santiapillai *et al.* 1982, Santiapillai *et al.* 1984) including one on the pig *Sus scrofa* (Santiapillai and Chambers 1980). However, there was no attempt to determine the age structure of the species concerned.

As much of the coastal section of the Park is short-grass prairie and population densities are high, it is possible to find skeletons of the large mammals which have died in that area without a disproportionate expenditure of labour. Searching is aided by the ground being firm and dry throughout the main dry season from July to early October. From 1981 through 1985, annual searches were made to find skulls, which resulted in a collection of over 300 specimens. It was found, initially in water buffalo (*Bubalus bubalis*) that the well marked annual pattern of wet and dry seasons was matched by corresponding layering in the cementum of the molar teeth with, as in the case of the herbivores of the African savannah (Grimsdell, 1973), dark lines in the cementum corresponding with periods of drought. With increasing experience it was found that the number of layers could also be determined in sambar deer (*Cervus unicolor*) and chital (*Axis axis*), where the main problem in counting resulted from irregularity in layering, and finally in the pig (*Sus scrofa*), where the main problem has been the frequency of a combination of a densely opaque white background coloration of the cementum with weakness of definition of the incremental lines. Despite the problems encountered, 85% to 95% of the molar teeth yielded counts of the number of layers in the four species involved. Preliminary accounts of the findings were published by Ashby and Santiapillai (1986), Ashby and Santiapillai (1991). Final publication was delayed in the expectation that further collection of material would permit calculation based on larger sample sizes, which was particularly desirable in the case of pig and chital. However, added to the difficulty of organizing collection of material in the field in the years since 1985, the epidemic of swine fever in 1989 (De Silva *et al.*, 1995) massively disturbed the age structure of the pig population. Therefore we decided to publish the data resulting from the skulls collected from 1981 through 1985 in the belief that the life table of the pig which has been constructed and the statistical data on resulting wear, though lacking in detail, are reliable in their broad characteristics.

Material and Methods

Material obtained in the annual searches of coastal dunes, grass prairies, margins of water holes and open bush was supplemented by specimens found by game guards in the course of patrols. In the case of the pig, sections were made initially of both canines and molar teeth and both dentine and cementum examined. Layering was evident in the dentine of both types of teeth in some individuals, but given that no consistent relationship was observed between numbers of layers and age as indicated by tooth-wear, it was concluded that layering in the dentine was not a good measure of age. Attention was therefore focussed, as in the ruminants studied, on layering in the cementum of the molar teeth. The technique of preparation, which had to be unsophisticated, was based on the method which had proved successful with water buffalo and deer. First lower molars were bisected vertically and transversely to give vertical sections of the cementum and dentine between roots. The surface of the cementum and dentine was polished successively with a coarse and a fine grade of carborundum powder and then examined under a 12 x handlens and a strong unidirectional light, normally sunlight. It was found helpful to examine the specimens with incident light from various angles. Initially the number of layers was counted in specimens where layering was clear. It was then extended to those where it was less easy to discern. In all specimens, several independent assessments were made. This process eventually left a **residium** where no count of layers was possible. In addition the depth of both dentine and cementum in the section were measured with a micrometer. Where available, the two lower first molars were used and average values for parameters calculated. Where this was not the case, attention concerning layering was turned to upper first molars and if necessary, to more posterior molars. But the depth of dentine and cementum were used in calculating regressions only from first molars.

Estimate was made of tooth-wear in all specimens, based on Schaller's (1967) nine point scale which had been devised with deer particularly in mind. While the wear pattern in pigs is not identical to that in ruminants, given the differences in tooth and jaw structure and functioning, it is believed that a parallelism between given wear-classes in ruminants and pigs was achieved. A key wear-class in the series is number III which occurs at the end of the subadult

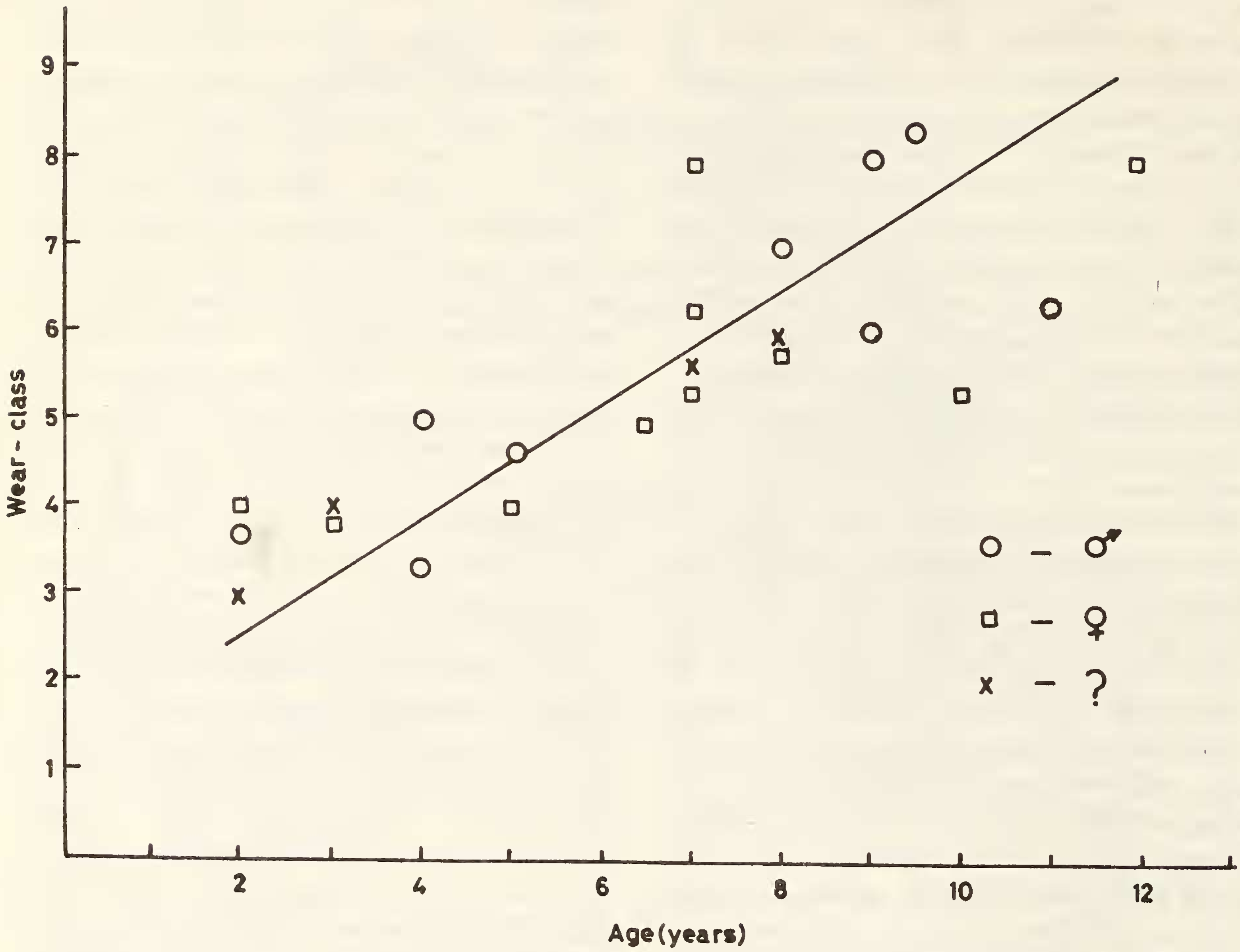

Fig. 2. Relation in wild pig (*Sus scrofa*) of wear of dentition to age as estimated from layering in dental cementum.

phase when the last molar is completing eruption. Analysis of data was simplified in the present instance by the fact that all the specimens found were already fully grown; where the whole of the lower jaw was available, its length provided confirmation of this fact. To make the estimation of tooth-wear more sensitive, each grade of wear was sub-divided into three, giving besides the typical expression of the class of wear (W), a W+ and a W- grading, with the + sign indicating one third progression towards the next older grade, and W- one third of a grade more youthful than the standard, giving effectively a 27 point scale. The most youthful specimen was judged to be in grade III.

Given that the tusks of males are larger than those of females, it was possible to judge the sex of specimens where canine teeth were present or at least the front end of the jaw was intact and therefore their sockets remained in cases where the canine had fallen out.

Results and Conclusions

There were 29 specimens with teeth present, and satisfactory sections of first or second molars were obtained in 27 of these. Estimates of age from layering were obtained in 23, and of depth of cement and of dentine in M1 in 20 specimens. For individuals where the two

Vertical section of cementum of M1 of wild pig with dentine above. Position of a main Dark Layer is marked by X and of an intermediate Dark Layer by an arrow. In this individual, faint intermediate lines were formed several times per year in its last years

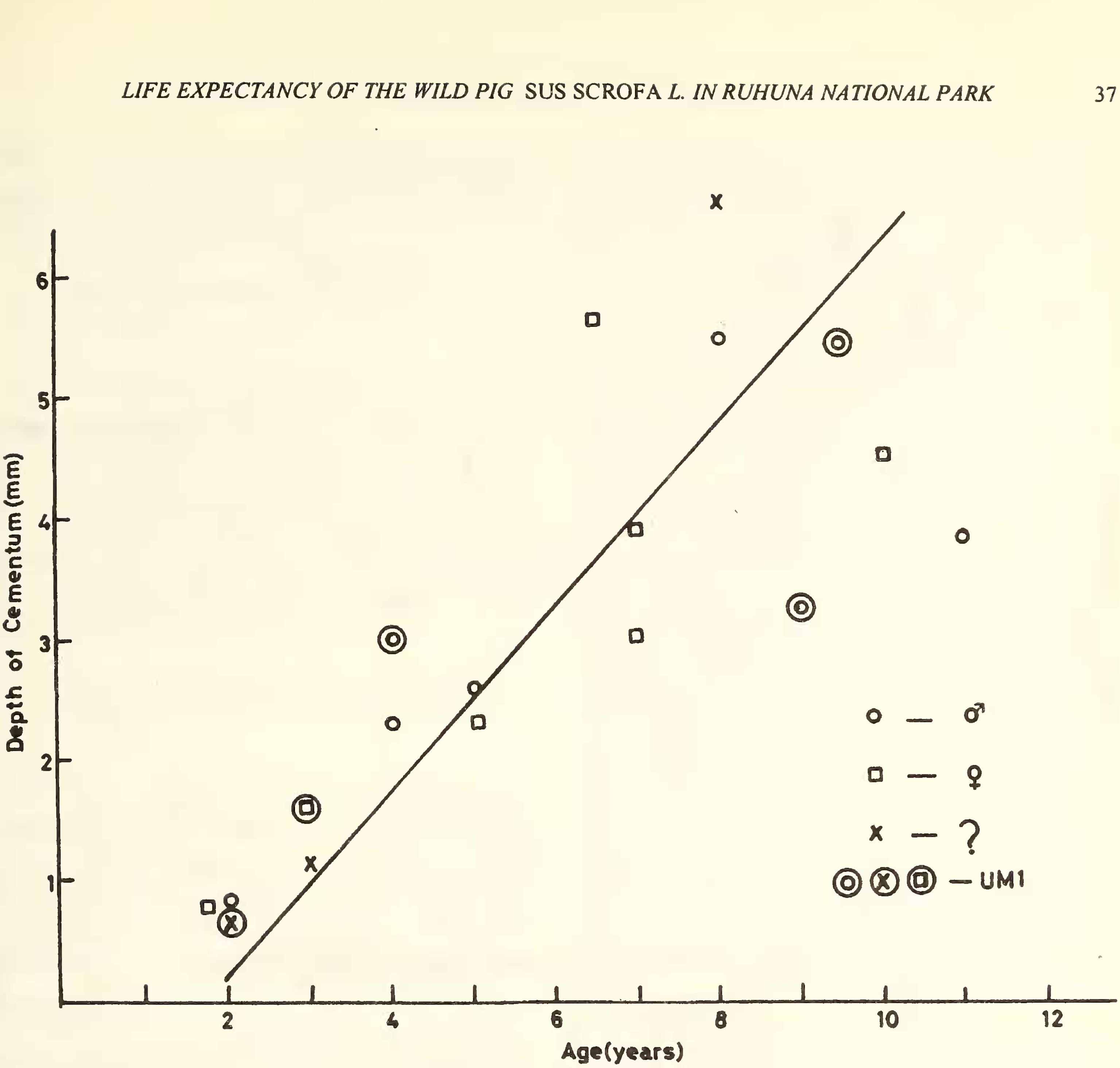

Fig. 3. Relation in wild pig of depth of cementum in bisected M1 to age as estimated from layering in cementum.

parameters concerned were determined, the relation of age as indicated by layering to wear-class is given in Fig. 2, its relation to depth of cementum in Fig. 3 and to depth of dentine in Fig. 4. In the absence of data from research, it has been assumed that the eruption of M1 is completed towards the age of one year and that cementum starts to form soon after eruption finishes. Since most births occur in March and April (Santiapillai and Chambers 1980) (although striped young are seen at other seasons), the first dark band in the cementum corresponding to the latter part of the main dry season, can be expected to form in M1 at about the age of one and a half years. It was therefore assumed that the age estimated from layering in M1 was the number of such layers plus one. Where both M1 and M2 were sectioned there was generally one more such layer in the cementum of M1 than in that of M2, therefore estimates of age based on M2 alone were calculated as the number of such layers +2.

In the specimens where layering is clearly shown (see Plate 1), there are faint dark layers in the cementum alternating with the main dark layers. This characteristic was apparent in most

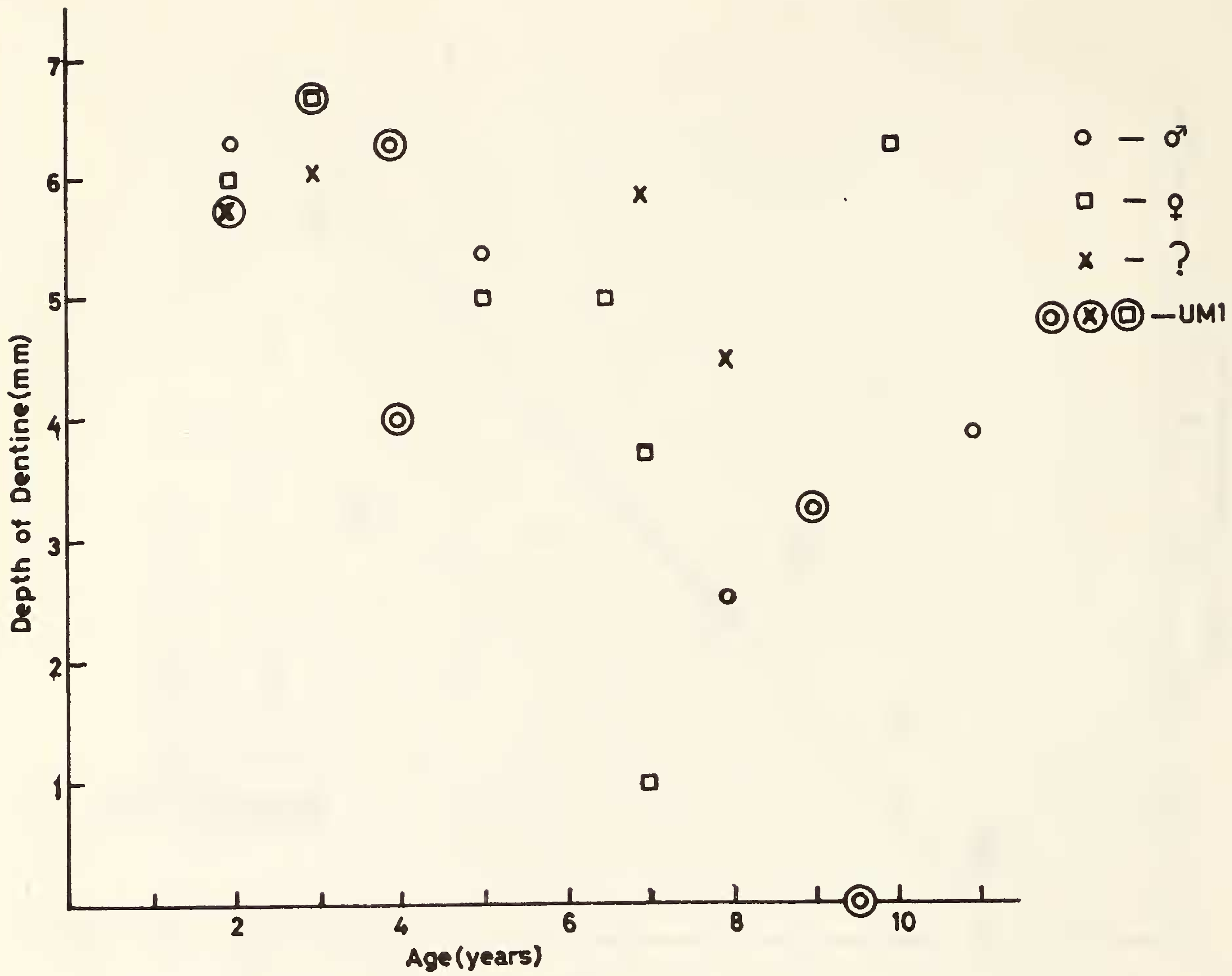

Fig. 4. Relation in wild pig of depth of dentine in bisected M1 to age as estimated from layering in cementum.

of the teeth in specimens of water buffalo, but in only a few specimens in deer species, and then only in old age. It was concluded that the faint dark layers correspond to the subsidiary dry season which occurs around February, and that it was much more prominent in buffalo than in deer because the former is a species grazing out in the open where the quality of forage is quickly affected by drought, whereas deer, more particularly sambar, are mainly browsers and feed on vegetation not much affected in quality by a short period of dry weather. The similarity of pig to buffalo in the pattern of layering may be attributed to its feeding mainly in open areas and at ground level and not on the shoots of shrubs or trees which, being deep-rooted, will be little affected by the short dry season. From Figs. 3 & 4, it will be seen that the rate of deposition of cement and of wear of dentine in upper M1 was not obviously different from that in lower M1 and the data from upper M1 teeth have therefore been included when calculating regressions. There was, likewise, no evidence of the relation of the various parameters differing in males and females. These conclusions applied also to water buffalo and sambar deer, and with the exception of a delayed start in cementum formation, to chital.

From Fig. 2, it is seen that there was a strong correlation between the estimates of wear and of age as estimated from layering, the regression equation for the range of age classes which occurred in the sample being:

Age = Wear Group x 1.53 - 1.96
r = 0.82

This compares with a value over the same range of wear-classes of r = 0.76 in water buffalo (N = 93), 0.83 (N = 77) in sambar deer, and 0.78 (N = 48) in chital for this relation. There was also a good overall correlation between depth of cement of M1 and number of annual layers as shown by Fig. 3. The regression equation with depth of cement (in mm) is:

Age = Cement depth x 0.13 + 1.93
r = 0.79

This compares with a correlation coefficient for the relationship of 0.92 in water buffalo, 0.89 in sambar deer and 0.74 in chital. There is a broader scatter of values in older pigs than in water buffalo and sambar, where the relationship of these parameters remains close throughout life.

In the relation between depth of dentine of M1 and age, it is seen from Fig. 4 that there are large differences in the rate of attrition of the dentine of M1 in different individuals inspite of the fact that for the overall dentition the relationship of wear to age is close. This feature was obvious on initial inspection of the specimens: individual teeth sometimes wore at considerably different rates, and such differences could occur within the length of individual molars. If individual variability is discounted, the data suggest that the rate of attrition of the dentine of M1 with increasing age is approximately linear. This pattern differs from that seen in the ruminants in this study. In these, wear was more markedly concentrated at the M1 level of the jaws than was the case in the pig: while the depth of dentine remained closely correlated with age, the rate of wear progressively lessened with time. In fact once eruption was completed, age as indicated by layering in M1 teeth of water buffalo and the two species of deer was proportional to the logarithm of the depth of the dentine.

Since there was no evidence of any marked difference in the life expectancy of the sexes, it is possible to construct an approximate life table for the pig based on the fairly small size of the sample of skulls obtained, and to compare it with those for the ruminants where samples were larger. The resulting curves deduced for the pig (N = 23) and that for water buffalo (N = 126) are given in Fig. 5. Since the youngest specimen of pig was at least 1.5 years old at death the present study gives no direct evidence of mortality prior to that age. However, its approximate value can be deduced from observational studies, given that the young pigs are easily seen and counted and not cryptic like the young of sambar deer. It is certain that neonatal and juvenile mortality is heavy and that predation by leopard (*Panthera pardus*) is an important cause. Eisenberg and Lockhart (1972) working in Wilpattu in a similar habitat, reported that 50% of the young pigs disappeared within one month of birth. Santiapillai and Chambers (1980) found that 75% of young pigs disappeared within one year. Since their study was based on visits made every three months, with the spring visit in May and the majority of births occurring in April, it can be concluded as an approximation that the young averaged one month of age when first seen. As a working hypothesis, it can therefore be concluded that mortality during the first thirteen months or so of life is in the order of seven eighths of those born. De Silva *et al.* (1995) give results in line with this conclusion.

From the data given in Fig. 5, it can be deduced that once the juvenile phase is past, the life expectancy of pig and water buffalo is similar. For individuals surviving at one year of age, the total mean life expectancy of the pig is 6.0 years, and of the water buffalo 5.6 years, with no evidence of a significant difference in this parameter between males and females. The

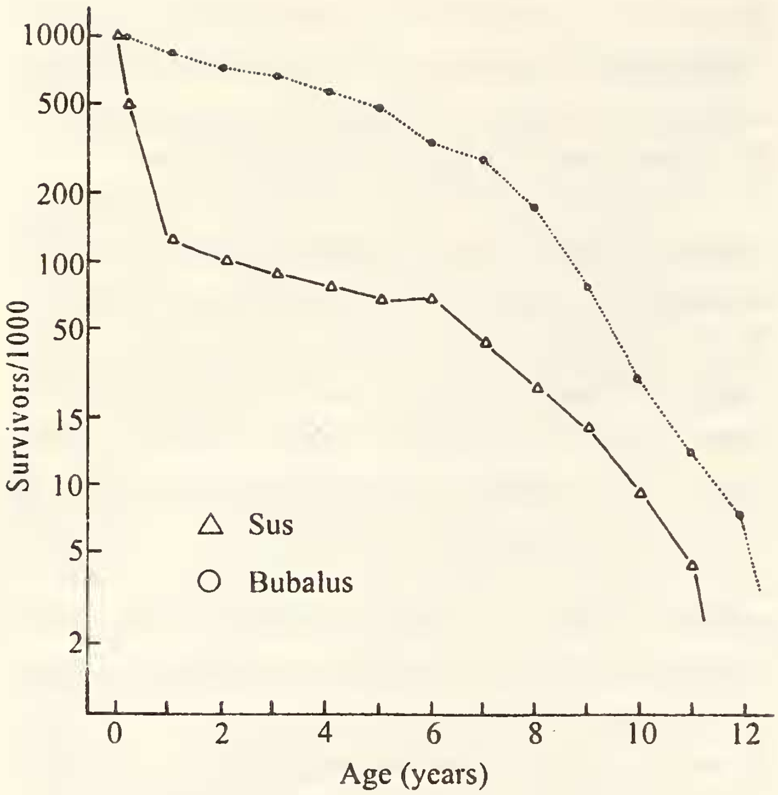

Fig. 5. Survival of wild pig compared with that of water buffalo (*Bubalus bubalis*) in Ruhuna National Park.

expected of length of reproductively active life in the females of the two species at Ruhuna is therefore similar, although perhaps rather longer in the pig than in the water buffalo as the former can give birth for the first time at 2 years of age and the buffalo at 3 years. The observed birth rate in the pig in Ruhuna National Park is in the order of 4 + per adult female per year, while in the water buffalo it is one per adult female per two years. On these data and assumptions, approximately 88% mortality in the pig when immature is balanced by a production of young per adult female which reaches maturity, eight times as great as in the water buffalo. Although the estimates are based on approximate data, the observations on juvenile mortality and on birth rate for the two species give concordant estimates and strengthen the likelihood that these are substantially accurate.

Discussion

The regime in Ruhuna National Park is one, like that in the savannahs of Africa, where predators take a large crop of herbivorous and polyphagous mammals of a size which they can profitably attack. The tiger (*Panthera tigris*) being absent from Sri Lanka, and leopard being the largest carnivore present and a solitary hunter, adults of water buffalo and probably also of sambar deer are too large to be predated. Water buffalo in good condition can also protect their young against the leopard. Its main prey, apart from juvenile pig, appears to include young and subadult chital, monkeys, and such medium sized species as the blacknaped hare (*Lepus nigricollis*). The juvenile pig may also be substantially at risk from the marsh crocodile (*Crocodylus palustris*) and the estuarine crocodile (*C. porosus*), which at Ruhuna National Park (RNP) though not growing to the size of crocodiles found in large rivers and other extensive water bodies, compensates for rather small individual bulk by their abundance in the larger water holes in the Park. As there appears to be little in the way of fish on which they can feed, their diet is dominated by corpses of animals which die nearby (which they drag into water within a few days, ending competition for the carrion from pigs), and the smaller of the mammals which come down to drink. Thus the pattern in RNP is for the largest of the herbivores, elephant and water buffalo, not to be substantially affected by predation at any age, while the young of the medium sized species, chital and more particularly the pig, suffer heavy predation prior to maturity and have a high juvenile mortality in consequence. Presumably the smaller mammals, apart from the bats and perhaps species like the Indian porcupine (*Hystrix indica*) with anti-predator devices, will suffer heavy predation at all stages of the life cycle, by the leopard and a variety of smaller predators.

The larger of the grazing mammals in RNP appear to be subject to a second important constraint affecting their life tables. Most of the oldest specimens of both water buffalo and pig, those approaching 12 years of age, had heavily worn dentition, and because of the reduction in